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"Single-Species Metapopulation Dynamics: A Structured Model"

M. GYLLENBERG
University of Luleå
Department of Applied Mathematics
S-951 87 Luleå
Sweden

These are preliminary lecture notes, intended only for distribution to participants.

Mats Gyllenberg

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Single-Species Metapopulation Dynamics: A Structured Model

Mats Gyllenberg
Department of Applied Mathematics
University of Luleå
S-951 87 Luleå, Sweden
and
Ilkka Hanski
Department of Zoology
University of Helsinki
P. Rautatiekatu 13
SF-00100 Helsinki, Finland

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Abstract. We describe and analyse a general metapopulation model, which consists of a model of local dynamics within a habitat patch and balance equations for dispersing individuals and the metapopulation. The model includes the effects of emigration and immigration on local dynamics. We derive the equilibrium population size distribution, which is skewed toward either small or large populations, depending on the relative magnitudes of local and metapopulation time scales. The model predicts a generally positive relationship between the fraction of occupied patches and the average local population size. Such a relationship has been commonly observed in nature. The model has the possibility for alternative stable equilibria, not found in models which ignore the effect of dispersal on local dynamics. We discuss the implications of our results for biological invasions and conservation biology.

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Luleå University of Technology
Department of Applied Mathematics
S-951 87 Luleå, Sweden

1 Introduction

Population ecological theory and practice have been largely restricted to the study of local dynamics of one or more species with either homogeneous interactions among individuals (most population ecological models; see e.g. May, 1981) or individuals aggregating at resource patches but mixing completely in each generation (Hassell, 1978; Hanski, 1981, 1987; Atkinson and Shorrocks, 1981; Shorrocks and Rosewell, 1987; Ives, 1988). Natural populations of most species have a hierarchical structure, several local populations comprising a metapopulation (Levins, 1969, Gilpin and Hanski, 1991). Local populations in a metapopulation are connected by dispersal, but it is not extensive enough to entirely obliterate generation-to-generation dynamics in local populations.

The metapopulation perspective has a long pedigree in population ecology (Andrewartha and Birch, 1954; den Boer, 1968), but much of the conceptual and mathematical development has relied on the very simplified "patch" models pioneered by Levins (1969). Levins (1969, 1970) assumed that the environment consists of discrete habitat patches that may support local populations. Levins's innovation was to simplify the description of metapopulation dynamics by ignoring changes in the sizes of local populations and instead focusing on the scalar variable, $p(t)$, the fraction of patches occupied at time t. This approach led to the ordinary differential equation

$$dp/dt = mp(1-p) - ep, \tag{1.1}$$

where m and e are colonization and extinction parameters, respectively. Eq.

(1.1) has served as a starting point for theoretical studies of single-species (Hanski, 1991, and references therein), competitive (Horn and MacArthur, 1972; Slatkin, 1974; Hanski, 1983) and predator-prey dynamics (Vandermeer, 1973; Hastings, 1977; Zeigler, 1977; see Taylor, 1988, for a review).

Equation (1.1) makes four major simplifying assumptions. First, the spatial arrangement of habitat patches and hence local populations is ignored. This assumption is difficult to relax without resorting to simulation techniques (DeAngelis et al., 1979; Ray et al., 1991). If dispersal occurs mostly among closely situated patches (stepping-stone dispersal), Eq. (1.1) overestimates colonization rate when p is small (Nisbet and Gurney, 1982). Secondly, Levins's model assumes that all patches are similar to each other, while in nature there is always variation in patch size and quality (Harrison, 1991). Thirdly, Eq. (1.1) ignores local dynamics, apart from the colonization and extinction events, and it therefore assumes implicitly that local dynamics occurs at a much faster time scale than the dynamics at the metapopulation level (Hanski, 1983). The fourth assumption is that local dynamics are not affected by emigration and immigration, conflicting with a wide range of observations from natural populations (Hanski, 1991, and references therein).

The last two simplifying assumptions of the Levins model (Table 1) may be relaxed by turning to the structured population theory in the spirit of Metz and Diekmann (1986) and by considering the total population as a metapopulation of local populations structured by population size. We start by modelling the local dynamics within a habitat patch and then derive balance equations for dispersing individuals and the metapopulation. Hastings and Wolin (1989)

have previously analyzed a structured metapopulation model, but they retained the Levins assumption of migration not affecting the dynamics of existing local populations (Table 1). We shall describe in Section 2 a general model which does not make this restrictive assumption, and we shall analyse the equilibria of this model in Section 3. To obtain more transparent results with clear biological interpretation we simplify the model in Section 4 by considering the limiting case in which local dynamics is much faster than metapopulation dynamics (Table 1). This simplified model still retains the role of migration in local dynamics, and it turns out that this is a more critical factor than the time scales of local and metapopulation dynamics in determining the qualitative behaviour of the metapopulation. Ecological predictions of our models are discussed in Section 5.

Table 1. Simplifying assumptions made in the models of Levins (1969), Hastings and Wolin (1989) and the present models, Sections 3 and 4. Note that all models ignore the spatial arrangement of habitat patches and assume that the patches are of the same size and quality.

Assumption	Model			
	Levins	Hastings and Wolin	Sect. 3	Sect. 4
Distinct times scales of local and metapopulation dynamics	Yes	No	No	Yes
Migration has no effect on local dynamics	Yes	Yes	No	No

2 The model

Throughout this paper, we use "population" for the local population occupying a discrete habitat patch and "metapopulation" for the set of extant local populations. We assume that there is a fixed number $\hat{N}$ of habitat patches, which may be empty or occupied. The size of a local population in an occupied patch is denoted by x, which is a number in $[1,\infty)$. ~~This interval is called the population space~~. The state of the metapopulation at time t is given by $n(t,x)$, the size distribution of local populations. Observe that $\int_{x_1}^{x_2} n(t,x)dx$ is the number of populations with size between x_1 and x_2 at time t. Therefore $N(t) := \int_1^\infty n(t,x)dx$ is the total number of occupied patches and $\hat{N} - N(t)$ is the number of empty patches at time t. We assume that local dynamics is density-dependent. Thus reproduction, mortality and emigration rates as well as the probability of local extinction depend on population size x.

We let $g(x)$ denote the intrinsic growth rate of a population of size x, due to reproduction and mortality only. Therefore, if one ignores migration and random catastrophies causing a local extinction, the population within a patch grows according to the ordinary differential equation

$$\frac{dx}{dt} = g(x).$$

This intrinsic growth may be logistic in which case $g(x) = rx\left(1 - \frac{x}{K}\right)$, but it may be something else as well.

We let $\gamma(x)$ denote the rate of emigration from a population of size x, and $q(t)$ the rate of immigration at time t. The immigration rate depends on the

number of dispersers and will be specified later. With these assumptions the growth of a population in an inhabited patch is governed by the equation

$$\frac{dx}{dt} = g(x) - \gamma(x) + q(t). \tag{2.1}$$

Per unit of time, $\int_1^\infty \gamma(x)n(t,x)dx$ individuals leave their patch and become dispersers searching for a new patch. We let ν denote the death rate of dispersers and α be the rate at which dispersers arrive at a patch. The balance equation for the number $M(t)$ of dispersers at time t thus reads

$$\frac{dM}{dt} = -(\alpha+\nu)M(t) + \int_1^\infty \gamma(x)n(t,x)dx. \tag{2.2}$$

We assume that dispersive individuals choose a new patch at random, and in particular that there is no inclination towards choosing either empty or inhabited patches. Per unit of time, $\alpha M(t)$ individuals arrive at a patch. Thus the immigration rate in Eq. (2.1) is $q(t) = \frac{\alpha M(t)}{\hat{N}}$. Finally, we assume that local populations may go extinct due to random catastrophies. Denoting the density-dependent catastrophy rate by $\mu(x)$ we obtain the balance equation

$$\begin{aligned} \frac{\partial}{\partial t}n(t,x) + \frac{\partial}{\partial x}\left(\left(g(x) - \gamma(x) + \frac{\alpha M(t)}{\hat{N}}\right)n(t,x)\right) \\ = -\mu(x)n(t,x). \end{aligned} \tag{2.3}$$

Colonization of empty patches is modelled by a boundary condition of the partial differential equation (2.3). The rate at which individuals arrive at

empty patches is given by $\alpha M(t)\frac{\hat{N}-N(t)}{\hat{N}}$. We assume that not every such colonization attempt is successful but that there is a probability ρ that the arriving individual survives and gives rise to a new population. Thus $\beta := \rho\alpha$ is the rate of successful colonization per disperser and proportion of empty patches. The flux through the boundary $\{1\}$ of the population state space $[1,\infty)$ must equal the colonization rate $\beta M(t)\left[1-\frac{N(t)}{\hat{N}}\right]$.
Thus

$$\left[g(1)-\gamma(1)+\frac{\alpha M(t)}{\hat{N}}\right]n(t,1)=\beta M(t)\left[1-\frac{N(t)}{\hat{N}}\right] \tag{2.4}$$

To make sense, the flux must be positive. To achieve this we make the natural assumption

$$g(1)-\gamma(1)>0,$$

that is, in small local populations birth dominates over death and emigration and the population tends to grow.

To simplify the equations we divide them by $\hat{N}$ and introduce the new variables $p(t,x) := n(t,x)/\hat{N}$, $P(t) := N(t)/\hat{N}$ and $D(t) := M(t)/\hat{N}$. Our model can now be written as follows:

$$\frac{\partial}{\partial t}p(t,x)+\frac{\partial}{\partial x}\Big(\big(g(x)-\gamma(x)+\alpha D(t)\big)p(t,x)\Big)=-\mu(x)p(t,x), \tag{2.5}$$

$$\big(g(1)-\gamma(1)+\alpha D(t)\big)p(t,1)=\beta D(t)\big(1-P(t)\big), \tag{2.6}$$

$$\frac{dD}{dt}=-(\alpha+\nu)D(t)+\int_1^\infty \gamma(x)p(t,x)dx, \tag{2.7}$$

$$p(0,x)=\phi(x), \tag{2.8}$$

$$D(0)=D_0, \tag{2.9}$$

where $\phi(x)$ is the initial size distribution of local populations and D_0 is the initial number of dispersers per total number of patches.

Equations (2.5) - (2.9) define a complicated system with nonlinearities both in the population growth rate and in the boundary condition. An extra complication is due to the fact that the population growth rate may change sign. Thus even results on existence and uniqueness of solutions are difficult. In this paper we shall not dwell on questions concerning existence and uniqueness but we shall concentrate on equilibrium solutions and their stability. A rigorous existence and uniqueness proof will appear in a forthcoming paper.

3 Existence of equilibria and the equilibrium population size distribution

We consider the existence of equilibria, that is time independent solutions $p(t,x)=p^*(x)$, $D(t)=D^*$ for all $t\geq 0$. We assume realistically that $g-\gamma$ is a concave function on $[1,\infty)$ with a unique maximum and that $\lim_{x\to\infty}\big(g(x)-\gamma(x)\big)=-\infty$. This assumption implies that for each level D^* of dispersers

there exists a unique population size $\hat{x} = \hat{x}(D)$ for which the growth rate is zero, that is

$$g(\hat{x}) - \gamma(\hat{x}) + \alpha D = 0 \tag{3.1}$$

holds (see Figure 3.1). If the size x of a local population is less than $\hat{x}(D)$ when there are D dispersers (per patch) the local population will grow, and if it is greater than $\hat{x}(D)$ it will decrease. $\hat{x}$ is called the *carrying capacity* of the patch. It is an increasing function of D. Conversely, D is an increasing function of $\hat{x}$ given by

$$D = \frac{1}{\alpha}[\gamma(\hat{x}) - g(\hat{x})]. \tag{3.2}$$

The carrying capacity of the trivial solution is denoted by $\hat{x}_0 := \hat{x}(0)$. $\hat{x}_0$ is the unique population size at which $g(\hat{x}_0) = \gamma(\hat{x}_0)$. Obviously $\hat{x}(D^*) > \hat{x}_0$.

Next we observe that at equilibrium we must have

$$p^*(x) = 0 \quad \text{for} \quad x > \hat{x}(D^*), \tag{3.3}$$

since if a population would have size $x > \hat{x}(D^*)$ it would shrink and since there is no input in the region $x > \hat{x}(D^*)$ this cannot be compensated for and hence $p^*(x)$ would change with time contradicting the assumption that it is an equilibrium. Hence (3.3) holds.

Putting $D(t) = D^*$, $\frac{dD}{dt} = 0$, and $p(t,x) = p^*(x)$ in Eq. (2.7) one obtains

$$D^* = \frac{1}{\alpha + \nu} \int_1^{\hat{x}(D^*)} \gamma(x) p^*(x) dx. \tag{3.4}$$

Similarily, (2.5) and (2.6) yield the *equilibrium population size distribution*

$$p^*(x) = \frac{\beta D^*(1 - P^*)}{g(x) - \gamma(x) + \alpha D^*} e^{-\int_1^x \frac{\mu(\xi)}{g(\xi) - \gamma(\xi) + \alpha D^*} d\xi} \tag{3.5}$$

where

$$P^* := \int_1^{\hat{x}(D^*)} p^*(x) dx. \tag{3.6}$$

Substituting (3.5) into (3.4) one obtains

$$D^* = D^* \frac{\beta}{\alpha + \nu}(1 - P^*) \int_1^{\hat{x}(D^*)} \gamma(x) \frac{1}{g(x) - \gamma(x) + \alpha D^*} e^{-\int_1^x \frac{\mu(\xi)}{g(\xi) - \gamma(\xi) + \alpha D^*} d\xi} dx. \tag{3.7}$$

The condition $D^* = 0$ obviously implies $P^* = 0$, so any nontrivial equilibrium must satisfy

$$R(D^*, P^*) = 1, \tag{3.8}$$

where

$$R(D,P) := \frac{\beta}{\alpha+\nu}(1-P)$$

$$\int_1^{\tilde{x}(D)} \gamma(x) \frac{1}{g(x)-\gamma(x)+\alpha D} \tag{3.9}$$

$$e^{-\int_1^x \frac{\mu(\xi)}{g(\xi)-\gamma(\xi)+\alpha D} d\xi} dx.$$

We call $R(D,P)$ the *net population reproduction number*. It has a very natural biological interpretation as has the relation (3.8). Let D and P be arbitrary but fixed. Consider a newly colonized patch. The mean number of dispersers this local population will produce during its lifetime (before it goes extinct due to a catastrophy) is given by

$$E(D) :=$$

$$\int_1^{\tilde{x}(D)} \gamma(x) \frac{1}{g(x)-\gamma(x)+\alpha D} \tag{3.10}$$

$$e^{-\int_1^x \frac{\mu(\xi)}{g(\xi)-\gamma(\xi)+\alpha D} d\xi} dx.$$

The probability that a disperser finds a patch before dying is $\frac{\alpha}{\alpha+\nu}$. The probability that the patch it arrives at is empty is $1-P$ and the probability that colonization is successful is ρ. Thus, on average, every newly colonized patch will give rise to $E(D)\frac{\alpha}{\alpha+\nu}(1-P)\rho = R(D,P)$ new local populations. Relation (3.8) says that a necessary condition for the existence of a nontrivial equilibrium is that this number equals one, that is, every local population exactly replaces itself.

In order to obtain another relation between D^* and P^* we substitute the expression (3.5) for $\mathbf{p}^*(x)$ into the definition (3.6) of P^*. This yields

$$P^* = \beta(1-P^*)D^*\ell(D^*), \tag{3.11}$$

where

$$\ell(D) := \int_1^{\tilde{x}(D)} \frac{1}{g(x)-\gamma(x)+\alpha D} e^{-\int_1^x \frac{\mu(\xi)}{g(\xi)-\gamma(\xi)+\alpha D} d\xi} dx \tag{3.12}$$

is the expected lifetime of a population given that the number of dispersers per patch is held fixed at D. Since $\beta(1-P^*)D^*$ is the colonization rate and P^* the proportion of occupied patches, (3.11) is an analogue of the wellknown relation in epidemiology: the prevalence of a disease equals the incidence rate times the duration of the disease.

The equations (3.8) and (3.11) represent curves in the D,P—plane. The points of intersection correspond to equilibria of the system (2.5) - (2.7). Eliminating P from(3.8) and (3.11) one finds the relation

$$\frac{1}{\alpha+\nu}E(D^*) = \frac{1}{\beta} + D^*\ell(D^*). \tag{3.13}$$

Once D^* has been solved from (3.13), P^* is obtained from (3.11).

Depending on the values of the parameters there can be none, one or several nontrivial equilibria.

Equation (3.1) (or equivalently (3.2)) defines a one-to-one correspondence between the number of dispersers per patch and the carrying capacity of a

patch. It is therefore possible to formulate the equilibrium conditions (3.8) and (3.11) in terms of the variables P and $\tilde{x}$ instead of P and D. This is preferable since $\tilde{x}$ but not D is measurable in the field, and since there exist extensive data on the relation between the proportion of occupied patches and the average size of local populations (for a review see Hanski et al. 1991). Moreover, if the local dynamics (reproduction, death and emigration) is fast compared with the dynamics at the metapopulation level (colonization and extinction), then most local populations will have a size close to $\tilde{x}$. This idea is elaborated further in the next section.

Letting

$$\tilde{E}(\tilde{x}) := E(D(\tilde{x})) = \tag{3.14}$$
$$\int_1^{\tilde{x}} \gamma(x) \frac{1}{g(x)-\gamma(x)-[g(\tilde{x})-\gamma(\tilde{x})]} e^{-\int_1^x \frac{\mu(\xi)}{g(\xi)-\gamma(\xi)-[g(\tilde{x})-\gamma(\tilde{x})]}d\xi} dx$$

and

$$\tilde{\ell}(\tilde{x}) := \ell(D(\tilde{x})) = \tag{3.15}$$
$$\int_1^{\tilde{x}} \frac{1}{g(x)-\gamma(x)-[g(\tilde{x})-\gamma(\tilde{x})]} e^{-\int_1^x \frac{\mu(\xi)}{g(\xi)-\gamma(\xi)-[g(\tilde{x})-\gamma(\tilde{x})]}d\xi} dx$$

Eqs. (3.8) and (3.11) turn into

$$\frac{\beta}{\alpha+\nu}(1-P^*)\tilde{E}(\tilde{x}^*) = 1, \tag{3.16}$$

and

$$\frac{\beta}{\alpha}(1-P^*)[\gamma(\tilde{x}^*)-g(\tilde{x}^*)]\tilde{\ell}(\tilde{x}^*) = P^*, \tag{3.17}$$

respectively. Eliminating P^* from (3.16) and (3.17) one finds the analogue of (3.13):

$$\frac{1}{\alpha+\nu}\tilde{E}(\tilde{x}^*) = \frac{1}{\beta} + \frac{1}{\alpha}[\gamma(\tilde{x}^*)-g(\tilde{x}^*)]\tilde{\ell}(\tilde{x}^*). \tag{3.18}$$

We close this section by a remark about the shape of the equilibrium population size distribution.

Since

$$\frac{dp^*}{dx} = \frac{\gamma'(x)-g'(x)-\mu(x)}{g(x)-\gamma(x)+\alpha D^*}p^*(x) \tag{3.19}$$

and $p^*(x)$ and $g(x)-\gamma(x)+\alpha D^*$ are positive in $[1,\tilde{x}^*)$ the zeros of $\frac{dp^*}{dl}$ coincide with those of $\gamma'(x)-g'(x)-\mu(x)$. It follows from our assumption about the concavity and behaviour at infinity of $g-\gamma$ that $\gamma'(x)-g'(x)$ is monotonically increasing, that $\gamma'(1)-g'(1)<0$ and that $0<\lim_{x\to\infty}(\gamma'(x)-g'(x))\leq\infty$. If we realistically assume that μ is nonincreasing, then it follows that $\frac{dp^*}{dx}$ has at most one zero in $[1,\tilde{x}^*)$. If it has no zero in $[1,\tilde{x}^*)$ then p^* will be monotonically decreasing and if $\frac{dp^*}{dx}$ has a zero, p^* will be decreasing for small population

N.B with $\gamma \to c\gamma$, $\gamma \to c\gamma$ $\frac{dp^*}{dx} = 0 \iff \gamma'(x) - g'(x) = \frac{1}{c}\mu(x)$

So as $c \to \infty$ $x \to$ set of $\gamma'(x)-g'(x)$

$\gamma(c) \leq x < \tilde{x}_c^* < \tilde{x}^*$

Case fig 5.1)

Also, as $c \to 0$ $x \to \infty$

sizes and increasing for large population sizes. We illustrate this in the case of logistic growth, emigration proportional to population density and density independent catastrophy rate. We thus assume

$$g(x) = rx(1 - \frac{x}{K}), \tag{3.20}$$

$$\gamma(x) = kx, \tag{3.21}$$

$$\mu(x) \equiv \mu. \tag{3.22}$$

Then the unique root of $\gamma'(x) - g'(x) - \mu(x) = 0$ is $x = \frac{K(r-k+\mu)}{2r}$.

Since

$$p^*(x) = \beta D^*(1 - P^*)e^{\int_1^x \frac{\gamma'(\xi) - g'(\xi) - \mu(\xi)}{g(\xi) - \gamma(\xi) + \alpha D^*} d\xi} \tag{3.23}$$

it follows that

$$\lim_{x \uparrow \tilde{x}^*} p^*(x) = \begin{cases} \infty & \text{if } \tilde{x}^* > \frac{K(r-k+\mu)}{2r} \\ \text{a positive constant} & \text{if } \tilde{x}^* = \frac{K(r-k+\mu)}{2r} \\ 0 & \text{if } \tilde{x}^* < \frac{K(r-k+\mu)}{2r}. \end{cases} \tag{3.24}$$

Thus the population size distribution is skewed towards large sizes if $\tilde{x}^* > \frac{K(r-k+\mu)}{2r}$ and towards small sizes of $\tilde{x}^* < \frac{K(r-k+\mu)}{2r}$. Observe that this condition cannot be written explicitly in terms of the parameters r, μ, k, ...,

since it depends on the solution $\tilde{x}^*$ of equation (3.18) which cannot be solved analytically. However $\tilde{x}^*$ is always greater than $\tilde{x}_0 := \frac{K(r-k)}{r}$, the carrying capacity corresponding to the trivial solution. So, if $\tilde{x}_0 > \frac{K(r-k+\mu)}{2r}$, that is, if $r - k > \mu$, then $\lim_{x \uparrow \tilde{x}^*} p^*(x) = \infty$ for all equilibrium states. But if $r - k < \mu$, then a more detailed analysis is necessary.

The situation is especially interesting in the case where there are two non-trivial equilibria. It is then possible that one equilibrium has $\lim_{x \uparrow \tilde{x}^*} p^*(x) = 0$ whereas the other has $\lim_{x \uparrow \tilde{x}^*} p^*(x) = \infty$. It is clear that the equilibrium with smaller $\tilde{x}^*$ has $\lim_{x \uparrow \tilde{x}^*} p^*(x) = 0$ and the one with bigger $\tilde{x}^*$ has $\lim_{x \uparrow \tilde{x}^*} p^*(x) = \infty$. At first sight one might think that the behaviour of $p^*(x)$ at $\tilde{x}^*$ would determine the stability of the equilibrium. The next example shows that this is not the case.

Example Let g, γ and μ be as in (3.20) - (3.22) with $r = \log 2$, $K = 1000$, $\mu = 0.4$, and $k = 0.5$. We assume that $\nu = 0$, $\alpha = 1$ and analyse the equilibria using ρ as a bifurcation parameter. Observe that $r - k = 0.19 < 0.4 = \mu$ so both $\lim_{x \uparrow \tilde{x}^*} p^*(x) = 0$ and $\lim_{x \uparrow \tilde{x}^*} p^*(x) = \infty$ are possible. Since $\frac{K(r-k+\mu)}{2r} \approx 428$, $p^*(x)$ will tend to zero as x tends to $\tilde{x}^*$ if $\tilde{x}^* < 428$ and $p^*(x)$ will tend to infinity as x tends to $\tilde{x}^*$ if $\tilde{x}^* > 428$.

The equation (3.18) was solved numerically for several different values of $\rho \in (0, 1]$. The results for $\rho = 0.01$, $\rho = 0.007$ and $\rho = 0.00533$ are represented in Fig. 3.2 to Fig. 3.4. For large values of ρ there are two nontrivial equilibria; one with $\tilde{x}^* < 428$ and the other with $\tilde{x}^* > 428$. As ρ decreases the carrying capacity $\tilde{x}^*$ of the two equilibria approach each other until they merge at

at $\tilde{x}^* \approx 515$ when ρ is approximately 0.00533. Thus the population size distribution corresponding to the equilibrium with smaller $\tilde{x}^*$ will change shape before the equilibrium reaches the bifurcation point. This happens when ρ is approximately 0.007. The bifurcation diagram is plotted in Fig. 3.5.

4 Derivation and analysis of a simplified model

In this section we shall return to the third simplifying assumption in the Levins model, namely that the local dynamics takes place on a much faster time scale than the dynamics at the metapopulation level. We shall replace in the system of (2.5) - (2.7), the intrinsic growth rate $g(x)$, the emigration rate $\gamma(x)$, the death rate ν of dispersers, and the rate α at which dispersers arrive at a patch, by $cg(x)$, $c\gamma(x)$, $c\nu$ and $c\alpha$, respectively, and analyse the limiting system obtained by formally letting $c \to \infty$. Note that since $\beta = \rho c\alpha$ this means that ρ has to tend to zero in such a way that β remains finite. Our approach will be intuitive rather than rigorous. A rigorous treatment of this singular perturbation procedure will appear in a forthcoming paper.

First note that integrating equation (2.5) from 1 to ∞ and taking the boundary condition (2.6) into account one obtains

$$\frac{dP}{dt} = \beta D(1-P) - \int_1^\infty \mu(x)p(t,x)dx. \tag{4.1}$$

Now make the replacement of parameters as described above. The dynamics of a local population is described by

$$\frac{1}{c}\frac{dx}{dt} = g(x) - \gamma(x) + \alpha D, \tag{4.2}$$

while the number of dispersers per patch obey the equation

$$\frac{1}{c}\frac{dD}{dt} = -(\alpha+\nu)D + \int_1^\infty \gamma(x)p(t,x)dx. \tag{4.3}$$

Letting $c \to \infty$ we infer from (4.2) that a population in a newly colonized patch will immediately grow to its carrying capacity $\tilde{x}$ determined by Eq. (3.1). This in turn implies that the population size distribution $p(t,x)$ will be a Dirac measure concentrated at $\tilde{x}$:

$$p(t,x) = P(t)\delta_{\tilde{x}}(x). \tag{4.4}$$

In the limit (4.3) therefore becomes

$$D = \frac{\gamma(\tilde{x})}{\alpha+\nu}P, \tag{4.5}$$

whereas (4.1) takes the form

$$\frac{dP}{dt} = \beta D(1-P) - \mu(\tilde{x})P. \tag{4.6}$$

The limiting system is thus given by the scalar ordinary differential equation (4.6) supplemented by (4.5) and (3.1) (or equivalently by (3.2)) which give the relations between P, D and $\tilde{x}$. To obtain the condition for equilibrium we put

$\frac{dP}{dt} = 0$ in (4.6) and replace D first by the expression given in (4.5) and then by the one given in (3.2). We get

$$\frac{\beta}{\alpha+\nu}(1-P^*)\frac{\gamma(\tilde{x}^*)}{\mu(\tilde{x}^*)} = 1, \tag{4.7}$$

$$\frac{\beta}{\alpha}(1-P^*)[\gamma(\tilde{x}^*) - g(\tilde{x}^*)]\frac{1}{\mu(\tilde{x}^*)} = P^*. \tag{4.8}$$

Observe that (4.7) and (4.8) are nothing but (3.16) and (3.17) with

$$\tilde{E}(\tilde{x}) = \frac{\gamma(\tilde{x})}{\mu(\tilde{x})} \tag{4.9}$$

and

$$\tilde{\ell}(\tilde{x}) = \frac{1}{\mu(\tilde{x})}. \tag{4.10}$$

This is exactly as it should be since if one performs the same limiting procedure as above in the definitions (3.14) and (3.15) one gets (4.9) and (4.19).

Eliminating P^* from (4.7) and (4.8) (or using (3.18) with the expressions (4.9) and (4.10) for $\tilde{E}(\tilde{x})$ and $\tilde{\ell}(\tilde{x})$, respectively) one finds

$$g(\tilde{x}^*) = \frac{1}{\rho}\mu(\tilde{x}^*) + \frac{\nu}{\alpha+\nu}\gamma(\tilde{x}^*). \tag{4.11}$$

By (4.5) and (3.1) D and $\dot{x}$ can be considered as functions of P only. We therefore denote the right hand side of (4.6) by $F(P)$. One has $F(0) = 0$ and $F'(0) = \beta\frac{\gamma(\tilde{x}_0)}{\alpha+\nu} - \mu(\tilde{x}_0)$. We therefore conclude that for small values of β the

trivial solution will be stable but it will loose its stability as β grows beyond the value $(\alpha+\nu)\frac{\mu(\tilde{x}_0)}{\gamma(\tilde{x}_0)}$. Moreover, since $F(1) = -\mu\left(\tilde{x}\,|_{P=1}\right) < 0$, we infer that if the trivial equilibrium is unstable, there is at least one stable nontrivial equilibrium. Also, neglecting the possibility of zeros of F with multiplicity greater than one, we see that if the trivial solution is stable there is an even number of nontrivial equilibria. The smallest one is unstable, the next stable and so on. In particular, if there are exactly two nontrivial equilibria the greater one is stable while the smaller one is unstable.

We shall now investigate the equilibria in more detail in the case of logistic growth of local populations, per capita emigration rate independent of population size and constant catastrophy rate. We thus choose g, γ and μ as in (3.20)-(3.22).

The equilibrium condition (4.7) and (4.8) is then equivalent to

$$\frac{\tilde{x}^*}{K} = \left(1-\frac{k}{r}\right) + \frac{k}{r}\frac{\alpha}{\alpha+\nu}P^*, \tag{4.12}$$

$$\tilde{x}^* = \frac{\mu}{\beta}\frac{(\alpha+\nu)}{k}\frac{1}{1-P^*} \tag{4.13}$$

These equations are identical to Eqs. (8) and (9) in Hanski (1991).

Next we shall investigate the solutions of (4.11). Assume first that μ is constant and $\nu = 0$. If $\tilde{x}_0 < \frac{K}{2}$ and if $\mu < g(\tilde{x}_0)$, then for $\rho < \frac{4\mu}{rK}$ there will be no solution, for $\frac{4\mu}{rK} < \rho < \frac{\mu}{g(\tilde{x}_0)}$ there will be two solutions and for $\frac{\mu}{g(\tilde{x}_0)} < \rho$ there will be one solution to (4.13) in the permitted region $\tilde{x} > \tilde{x}_0$. (see Figure

4.1). As noted above the greater nontrivial solution corresponds to a stable and the smaller one to an unstable equilibrium. Thus we have the bifurcation diagram shown in Figure 4.2.

If, on the other hand, $\tilde{x}_0 > \frac{K}{2}$ (relatively low emigration rate), then there can never be more than one solution to (4.13) in $\tilde{x} > \tilde{x}_0$ (Figure 4.3). The bifurcation diagram for this situation is sketched in Figure 4.4.

However, these results are based on the assumption that μ is constant. In nature the probability of local extinction generally decreases with increasing population size (Williamson 1981, Diamond 1984, Schoener 1985, Schoener and Spiller 1987) and in this case there can be multiple equilibria even for $\tilde{x}_0 > \frac{K}{2}$. If γ and μ are as indicated in Figure 4.5, there are again two nontrivial equilibria and a bifurcation diagram similar to the one shown in Figure 4.2.

If ν is positive but small the above results remain qualitatively the same.

5 Discussion

Our results make testable predictions about three aspects of metapopulation dynamics: the distribution of local population sizes; the relationship between average local population size and the fraction of occupied habitat patches; and alternative stable equilibria. We discuss these three issues in turn.

The general model in Section 3 predicted a skewed distribution of population sizes, but depending on the magnitudes of local and metapopulation times scales, most populations were predicted to be either large (fast local dynamics) or small (slow local dynamics, in comparison with the rate of change at the metapopulation level). Hastings and Wolin (1989) concluded from their

structured metapopulation model that small local populations are always more numerous than large ones. This conclusion was however based on a number of unrealistic assumptions, including exponential growth of local populations. Assuming the logistic model for local dynamics, as we have done, it is clear that there must be a possibility for most populations being close to the environmental carrying capacity and hence being large. Unfortunately, there are two major problems in testing the prediction about population size distribution. First, unlike assumed in our model, habitat patches are rarely if ever of the same size in nature (Harrison 1991), hence the local carrying capacities vary and increase differences in the sizes of local populations. Second, our model is deterministic, apart from the local extinction events, while stochastic variability in population size is a pervasive feature of practically all natural populations (Hanski 1990). These considerations point to two important directions in which the present type of metapopulation model should be developed.

One of the few broadly valid generalizations in population ecology is the finding that the more widely distributed species tend to be locally more abundant than species with a more restricted distribution (Hanski 1982, Brown 1984, Gaston and Lawton 1990). This relationship between distribution and abundance has been found at all spatial scales (Hanski et al. 1991), but as emphasized by Brown (1984), one should compare only species which share the same basic ecology. In terms of the present model, this generalization says that there should be a positive relationship between $\tilde{x}^*$ and P^*.

Let us assume an assemblage of species in which the species differ from each other in only one of the following parameter combinations, $1 - k/r$, $\mu/\beta k$ or

$\alpha/(\alpha+\nu)$. It is clear from Eqs. (4.11) and (4.12) that if the species show variation in only the first or the second combination of parameters, there exists a positive relationship between $\hat{x}^*$ and P^* among the species. If the species show variation in $\alpha/(\alpha+\nu)$, both (4.11) and (4.12) are affected, but once again consequent changes in $\hat{x}^*$ and P^* are positively correlated. In terms of the original parameters, only interspecific variation in k does not necessarily give a positive relationship between $\hat{x}^*$ and P^*. Our hypothetical species assemblage in which the species differ in only one of the above parameter combinations corresponds to Brown's (1984) assemblage of species which are ecologically similar in most respects. Single-species metapopulation dynamics may therefore explain the positive relationship between distribution and abundance of species.

If several different parameters are varied at the same time in our model, it is possible to generate a species assemblage in which there is a negative relationship between $\hat{x}^*$ and P^*. Consider two contrasting sets of species, some with small k/r but large μ/β, while others have large k/r (but < 1) but small μ/β and small $\alpha/(\alpha+\nu)$ (Fig. 5.1). The former species tend to have relatively large local populations even if they have a restricted equilibrium distribution (small P^*), while the latter species show the opposite characteristics. Arita et al. (1990) have recently reported a negative relationship between distribution and abundance in Neotropical forest mammals. Their result is essentially due to large mammals having low densities but wide distributions, while smaller species tend to have more restricted distributions but are often locally abundant. This is consistent with our results: large species have larger k/r (high dispersal rate in relation to their intrinsic growth rate) but

probably smaller μ/β than small species (large species are less affected by environmental stochasticity). Metapopulation dynamics may thus explain both the usual positive (Gaston and Lawton 1990) as well as exceptional negative relationships between distribution and abundance.

One relatively easily testable prediction is that, for a given average local abundance ($\hat{x}^*$), species with high dispersal rate should have a wider distribution (larger P^*) than less dispersive species. Table 5.1 shows that this is the case in butterflies in the United Kingdom. The other explanations of the positive relationship between distribution and abundance (Hanski et al. 1991) do not make this prediction.

The simplified model analysed in Section 4 demonstrated that single-species metapopulation dynamics may have alternative stable equilibria. This is contrary to what Hastings and Wolin (1989) concluded from their model. The difference in our results is due to Hastings and Wolin's (1989) assumption that migration has no effect on the dynamics of existing local populations (see Table 1). Indeed, setting $\alpha = 0$ in Eq. (4.11) demonstrates that no alternative stable equilibria are possible in our model either without the influence of immigration on local dynamics. Two other metapopulation models that manifest the possibility for alternative stable equilibria (Hanski 1985, Roughgarden and Iwasa 1988) also incorporate the influence of immigration on local dynamics.

There are two distinct mechanisms that may create alternative stable equilibria in our model. First, for density-independent extinction probability (μ), alternative stable equilibria are possible if dispersal rate is high. When the metapopulation is small (small P^*), most patches are empty and most dis-

persers will die without leaving any offspring, because the probability of successful colonization of and reproduction in empty patches is much smaller than the probability of arriving at a patch ($\beta << \alpha$). Therefore, a small metapopulation may decrease in size (P^* approaches 0). On the other hand, when the same metapopulation is large (large P^*), most dispersers will land on occupied patches and will have, on average, a greater success of reproduction than when P^* is small. The metapopulation may now increase in size toward a stable internal equilibrium. These considerations are relevant for the much-studied question about the critical minimum size of a habitat patch that may support a local population, given that a fraction of offspring always dispersers away from the patch (Okubo 1980 and references therein). If several such patches are connected to each other, the critical patch size for population survival is decreased due to mutual migration, though there may exist alternative stable equilibria. If dispersing individuals move preferentially to occupied than unoccupied patches ('conspecific attraction'; Ray et al. 1991), the domain of alternative stable equilibria is decreased, but so is the value of P^*, because conspecific attraction decreases the rate of colonization of empty patches (Ray et al. 1991).

The above scenarios deal with highly dispersive species (large k). Alternative stable equilibria are possible also in the case of relatively sedentary species, if the extinction probability (μ) decreases with population size, as is nearly universally observed (Schoener and Spiller 1987 and references therein). We therefore conclude that alternative stable equilibria in metapopulation dynamics should not be dismissed for any species.

Alternative stable equilibria are an important consideration in conservation biology, because they create the possibility that a species crashes suddenly to regional extinction from a relatively high regional abundance (if it happens to cross the unstable equilibrium; Hanski 1985, Hastings 1991). Conversely, alternative stable equilibria make a regional invasion by a species more difficult, in the same manner as various (local) Allee effects hinder the establishment of local populations. The existing models of regional invasion deal with the parameters of local dynamics, such as lamda, f and K (MacArthur and Wilson 1967, Ebenhardt 1991). If metapopulation dynamics plays an important role, success of regional invasion may equally depend on rates of emigration (k), immigration (α), colonization (β) and extinction (μ). Comparative investigations of species' invasion abilities should therefore include also the latter set of parameters, which they do not do at present.

Conservation biologists attempting the re-establishment of extinct species in their natural environment should also pay attention to possible metapopulation effects. To increase the survival and reproductive success of dispersers, it would often be better to introduce the species simultaneously into several closely situated habitat patches than to equally many far-away patches. One example where such considerations are potentially important is the re-establishment of the critically endangered black-footed ferret Mustela nigripes in North America (Clark et al. 1987, Brussaard and Gilpin 1989).

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Legends

Figure 3.1 The function $y = g(x) - \gamma(x)$ and the definition of the carrying capacity $\tilde{x}(D)$

Figure 3.2 The curves 1. $y = E(\tilde{x}^*)$ and 2. $y = \frac{\alpha+\nu}{\alpha}\left(\frac{1}{\rho} + \frac{1}{\mu}(\gamma(\tilde{x}^*) - g(\tilde{x}^*)\right)$ in the case of logistic growth with $r = \log 2$, $K = 1000$, $\mu = 0.4$, $k = 0.5$, $\nu = 0$, $\alpha = 1$ and $\rho = 0.01$

Figure 3.3 The curves 1. $y = E(\tilde{x}^*)$ and 2. $y = \frac{\alpha+\nu}{\alpha}\left(\frac{1}{\rho} + \frac{1}{\mu}(\gamma(\tilde{x}^*) - g(\tilde{x}^*)\right)$ in the case of logistic growth with $r = \log 2$, $K = 1000$, $\mu = 0.4$, $k = 0.5$, $\nu = 0$, $\alpha = 1$ and $\rho = 0.007$

Figure 3.4 The curves 1. $y = E(\tilde{x}^*)$ and 2. $y = \frac{\alpha+\nu}{\alpha}\left(\frac{1}{\rho} + \frac{1}{\mu}(\gamma(\tilde{x}^*) - g(\tilde{x}^*)\right)$ in the case of logistic growth with $r = \log 2$, $K = 1000$, $\mu = 0.4$, $k = 0.5$, $\nu = 0$, $\alpha = 1$ and $\rho = 0.0053$

Figure 3.5 Bifurcation diagram in the case of logistic growth with $r = \log 2$, $K = 1000$, $\mu = 0.4$, $k = 0.5$, $\nu = 0$, $\alpha = 1$. Solid lines indicate stable equilibria and dashed lines unstable equilibria

Figure 4.1 The curves 1. $y = \gamma(\tilde{x})$, 2. $y = g(\tilde{x})$, and 3. $y = \frac{\mu}{\rho}$.

Figure 4.2 Bifurcation diagram in the case of logistic growth with constant μ, $\nu = 0$, $\tilde{x}_0 < \frac{K}{2}$, and $\mu < g(\tilde{x}_0)$. Solid lines indicate stable equilibria and dashed lines unstable equilibria

Figure 4.3 The curves 1. $y = \gamma(\tilde{x})$, 2. $y = g(\tilde{x})$, and 3. $y = \frac{\mu}{\rho}$

Figure 4.4 Bifurcation diagram in the case of logistic growth with constant μ, $\nu = 0$, $\tilde{x}_0 < \frac{K}{2}$, and $\mu < g(\tilde{x}_0)$. Solid lines indicate stable equilibria and dashed lines unstable equilibria

Figure 4.5 The curves 1. $y = \gamma(\tilde{x})$, 2. $y = g(\tilde{x})$, and 3. $y = \mu(\tilde{x})$

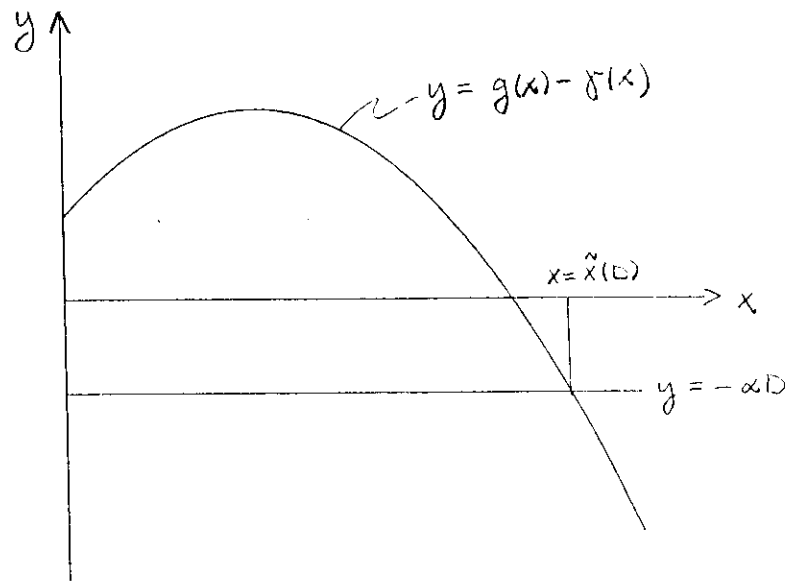

Figure 3.1

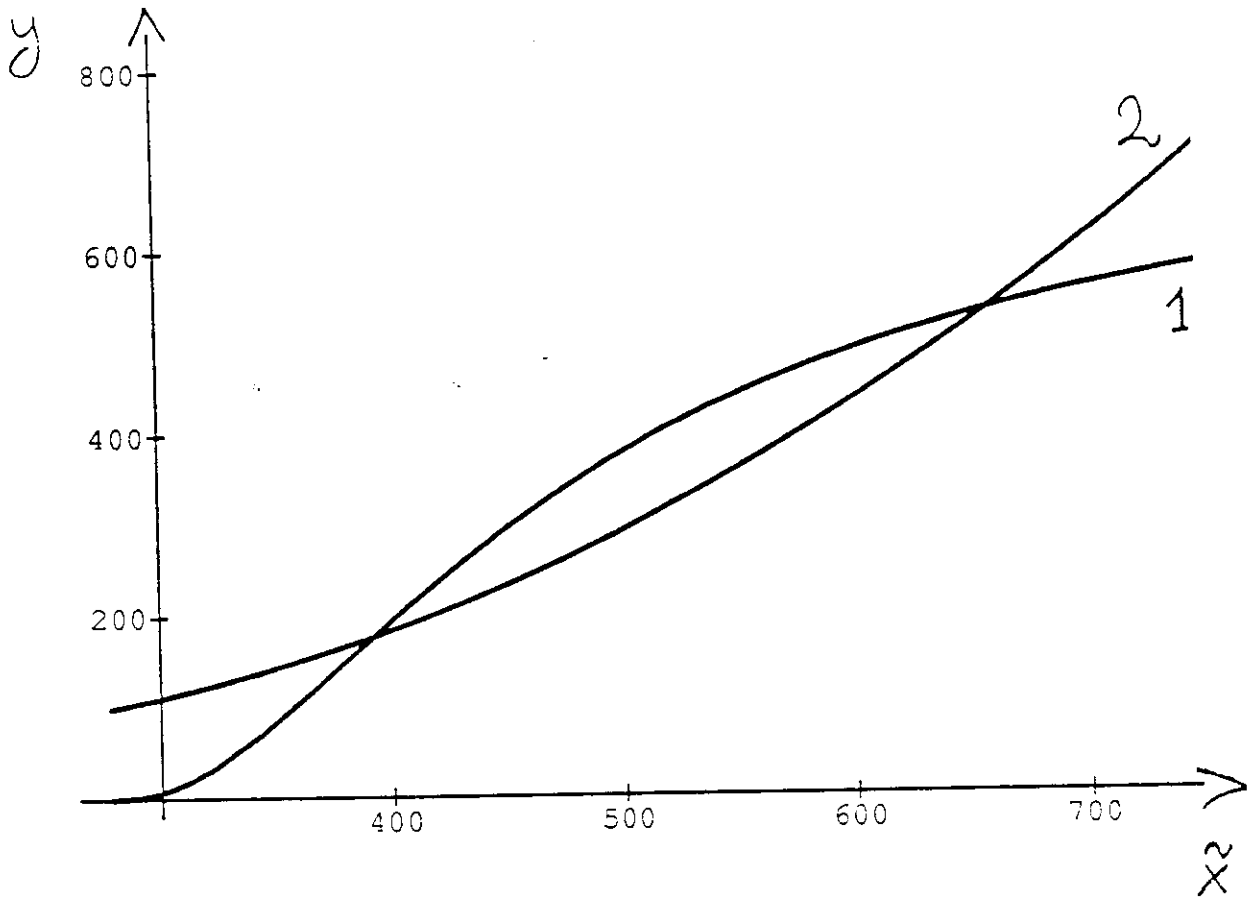

Figure 3.2

fig 3.2

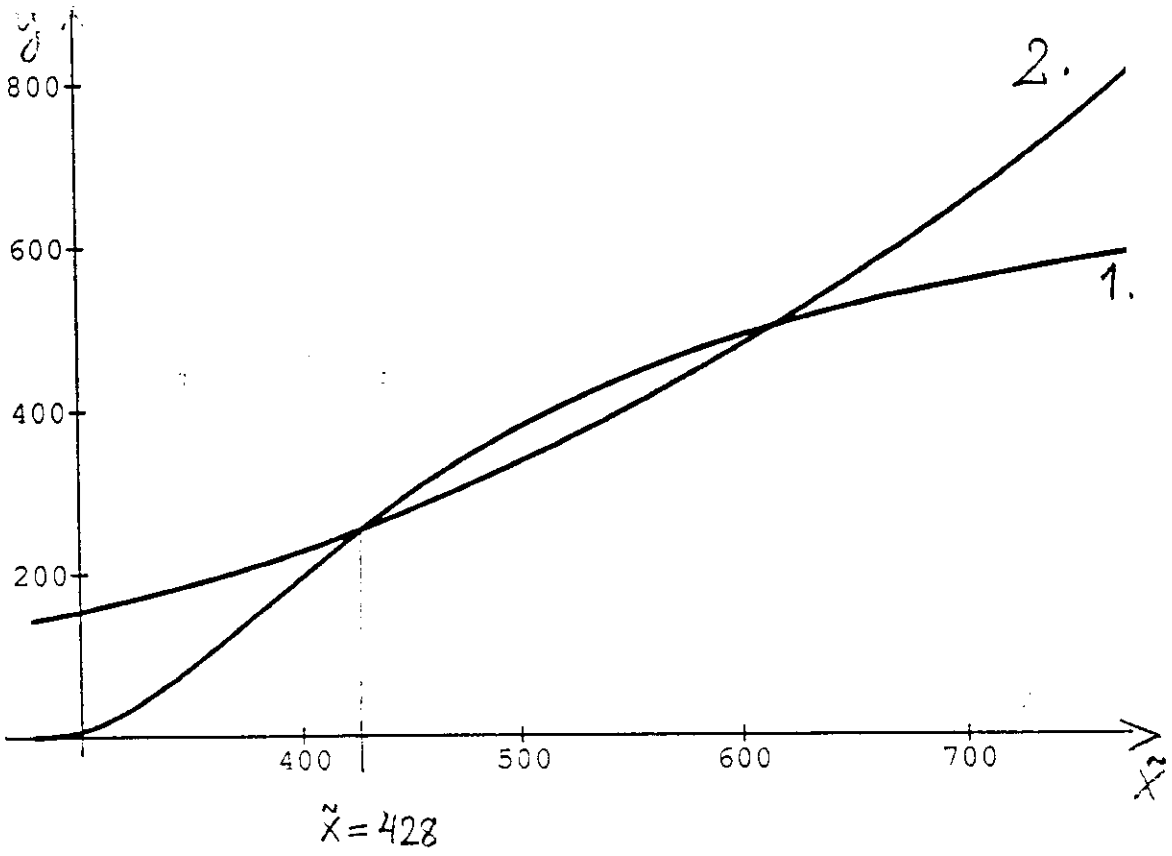

Figure 3.3

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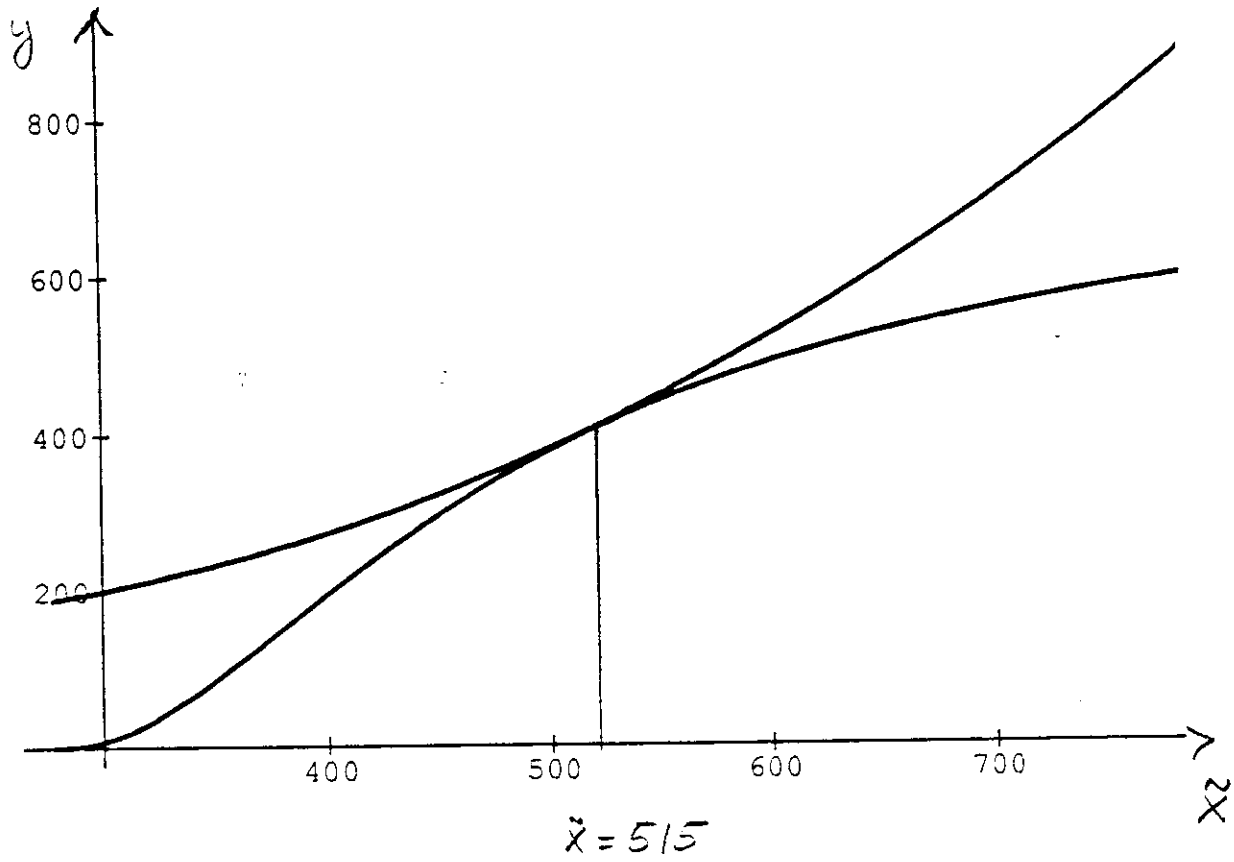

Figure 3.4

$\xi = 0.0053$

fig 3.4

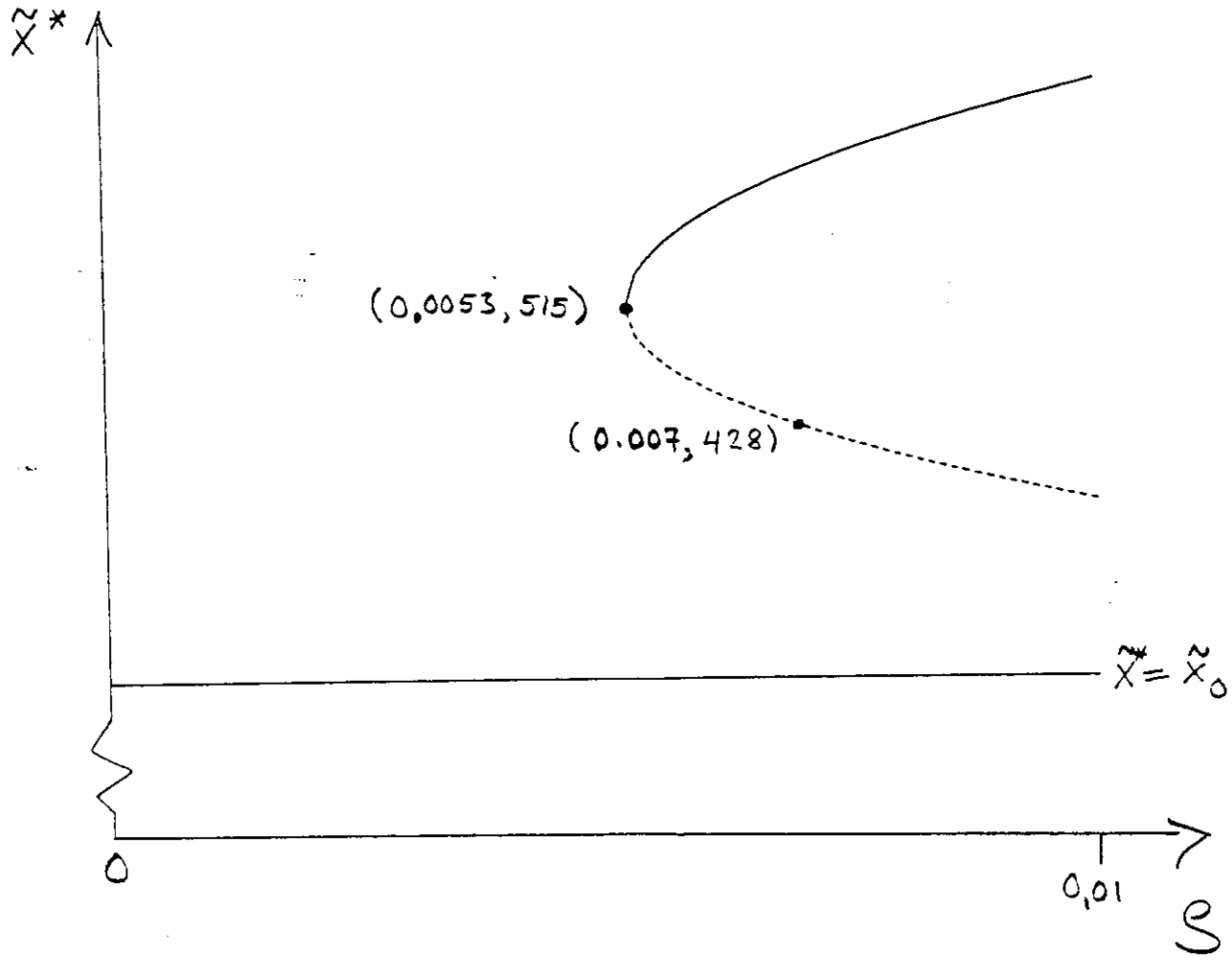

Figure 3.5

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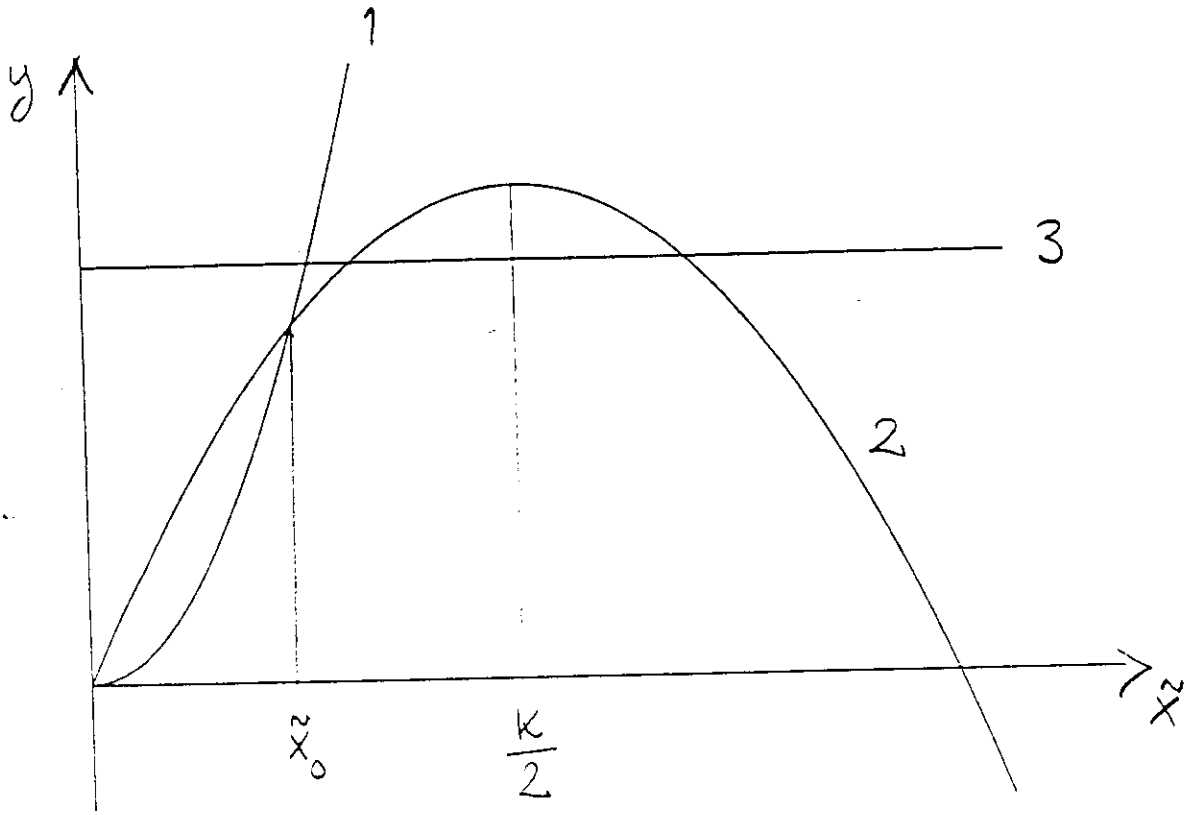

Figure 4.1

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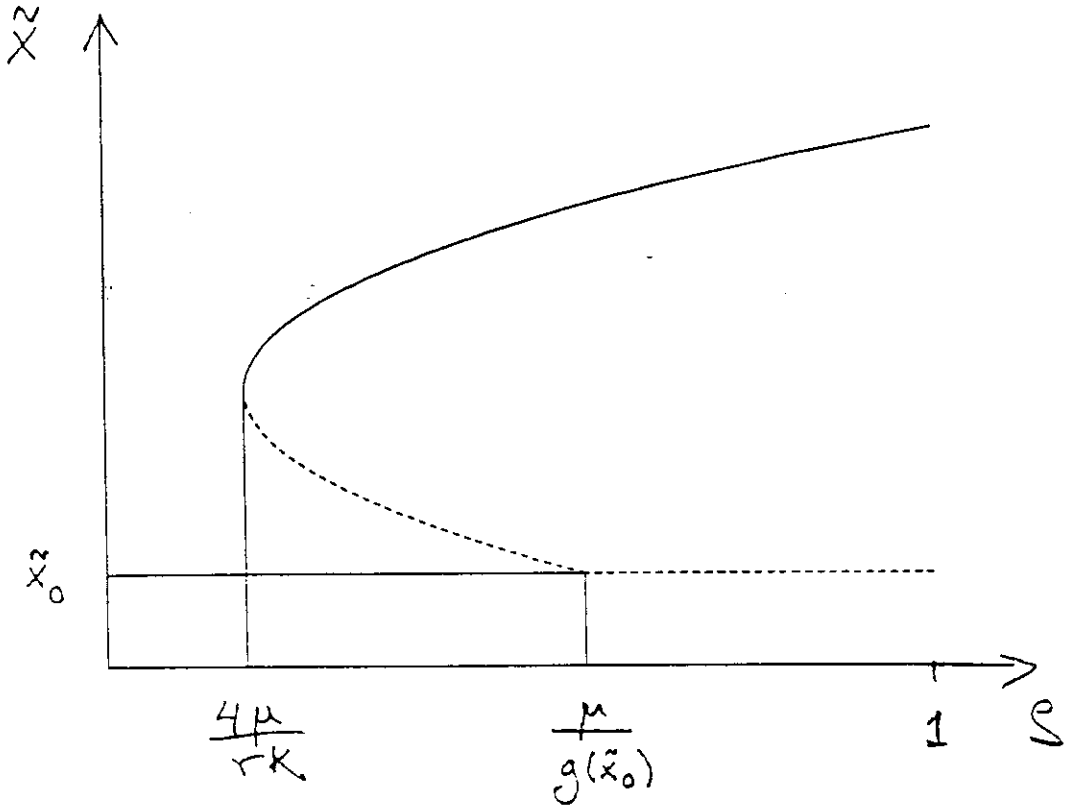

Figure 4.2

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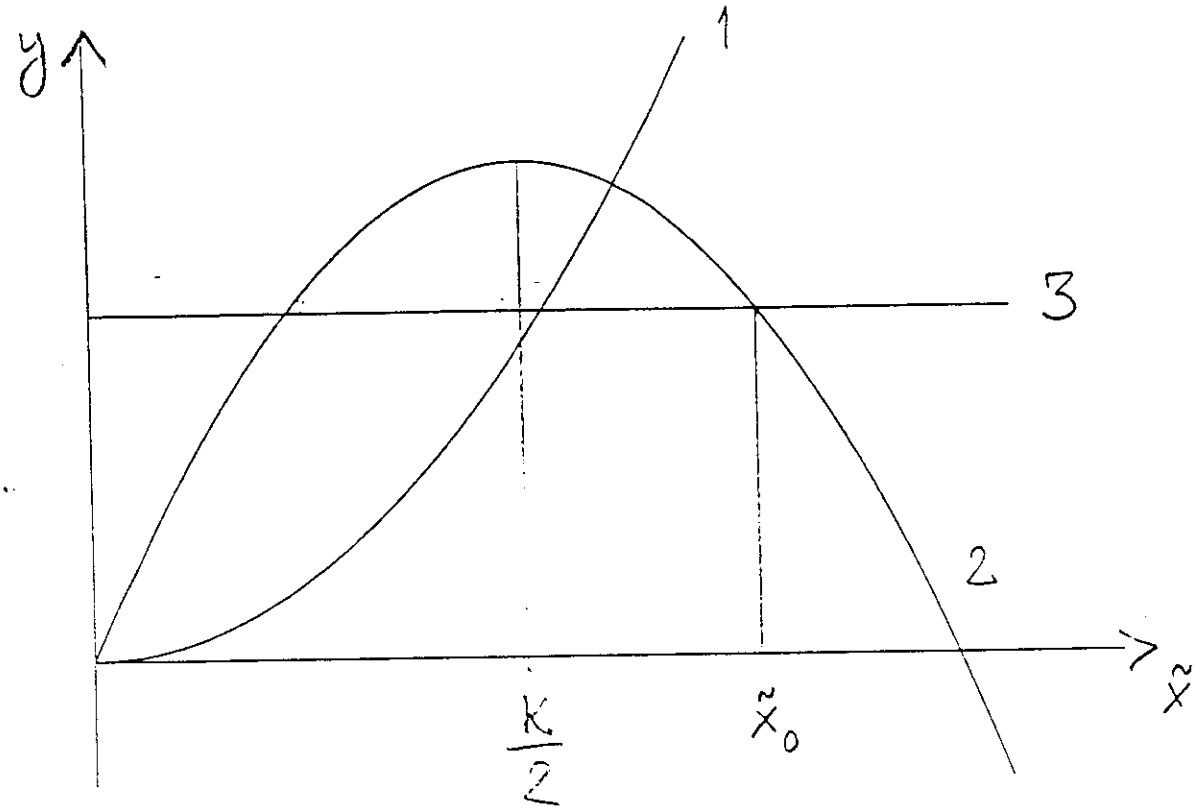

Figure 4.3

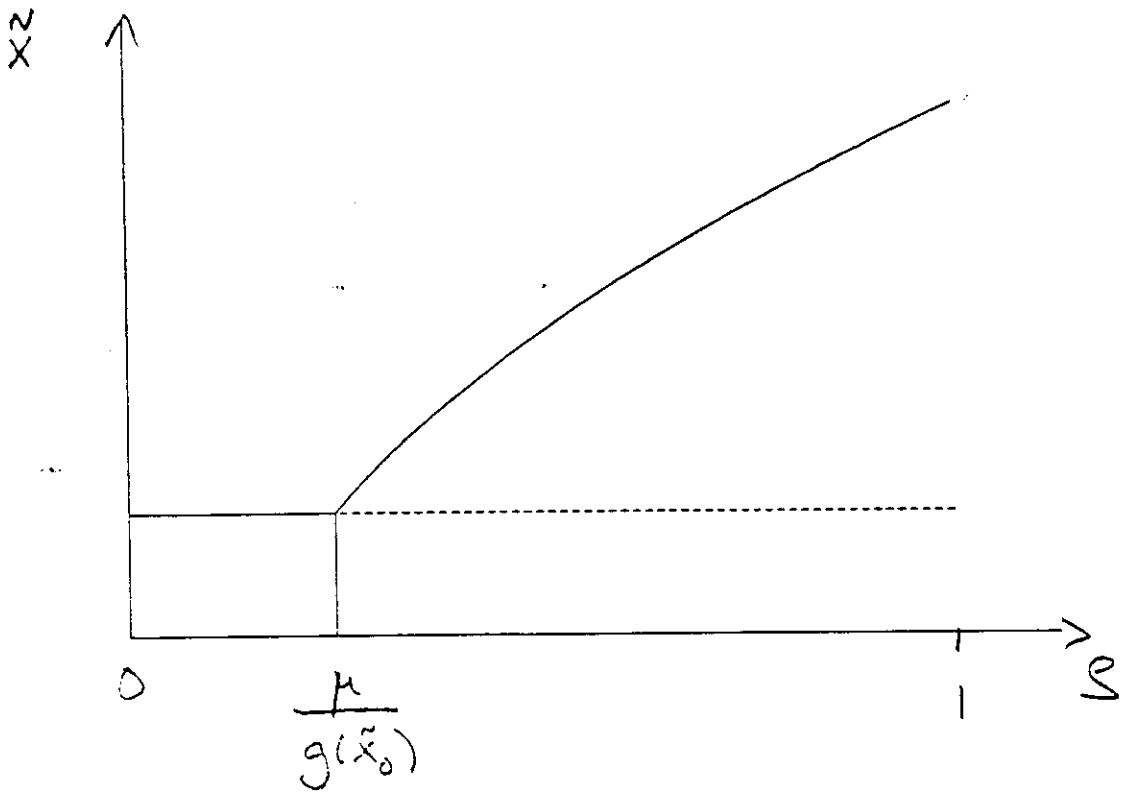

Figure 4.4

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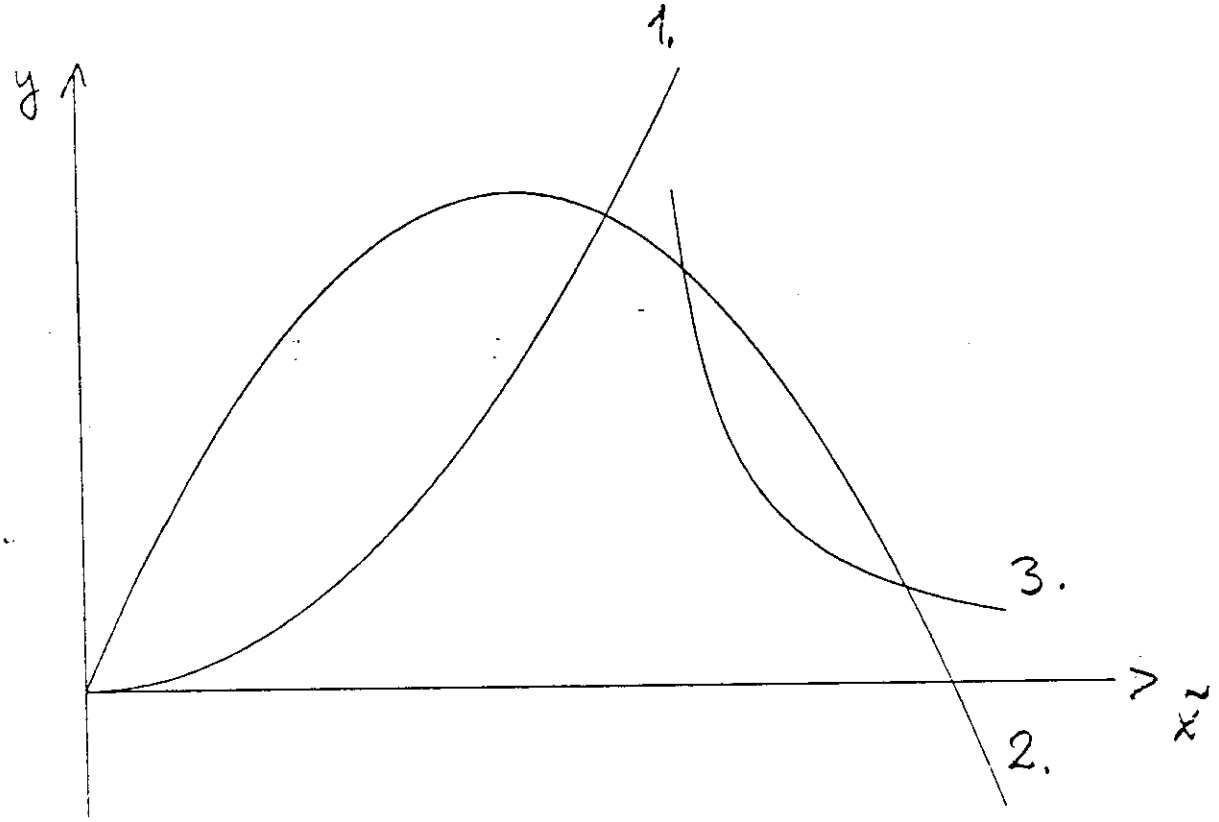

Figure 4.5

fig 4.5